

最优气孔行为理论和气孔导度模拟

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摘要 气孔调节功能是陆地生态系统碳-水耦合过程中最重要的环节。与即时的气孔导度测量相比, 气孔导度斜率能有效地反映气孔导度对CO₂浓度、饱和水汽压亏缺和光合作用的敏感性, 包含了环境因子对光合作用和临界水分利用效率等的综合影响, 为研究全球变化下陆地生态系统碳-水耦合关系提供了一个简明且综合的框架。气孔导度模型从经验模型、半经验模型发展到机理模型, 经过很多学者的改进, 但是模型参数的生物学意义和变化规律还不明确。鉴于气孔导度斜率方面研究的重要性和研究的不足, 为了加强对气孔导度调节规律的认识, 并减少气孔导度模拟的不确定性, 该文主要综述了长期以来国内外关于最优气孔行为理论和气孔导度模拟方面的研究成果, 其中包括广泛使用的气孔导度模型及参数意义, 讨论影响气孔导度斜率的主要因素以及气孔导度机理模型的应用, 并对最优气孔行为理论和气孔导度模拟方面的研究做了简单展望。

关键词 气孔导度斜率; 碳水耦合; 最优气孔导度理论; 气孔导度模型; 临界水分利用效率

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Optimal stomatal behavior theory for simulating stomatal conductance

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Abstract

Among the most critical processes in simulating terrestrial ecosystem performance is the regulatory role of stomata in carbon and water cycles. Compared with field measurements, the changes in stomatal slope caused by the biophysical environment provide a simple but effective synthetic framework for studying climate-related carbon and water cycling, due to its sensitivity to CO₂, vapor pressure deficit, and photosynthesis. It is also crucial in understanding the effects of climate change on photosynthesis and water use efficiency. Endeavored by numerous scholastic efforts, stomatal conductance models have been improved based on experimental, semi-experimental, and mechanical processes. However, the underlying biological mechanisms and the dynamics of key parameters in these models remain unexplored, especially regarding the changes in stomatal slope. By improving the understanding of the stomata's regulatory role, we reduced the uncertainty of stomatal conductance simulation. We then synthesized the recent developments and lessons in optimal stomatal behavior theory to simulate stomatal conductance and included an introduction to widely used stomatal conductance models and parameters, the main factors influencing stomatal slopes, and applications of the mechanical stomatal conductance models in different ecosystems. Based on our literature review, we proposed that future research is needed on the optimal stomatal behavior theory and its applications in simulating stomatal conductance.

Key words stomatal slope; carbon water coupling; optimal stomatal behavior theory; stomatal conductance models; marginal water use efficiency

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近年来, 森林生理生态学中的一个热点领域就是对碳、水循环紧密耦合的机理过程的研究(于贵瑞

等, 2004; 曹生奎等, 2009)。气孔是植物控制叶片与大气之间碳、水交换的重要门户, 气孔导度模拟是精

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确模拟陆地生态系统碳-水循环过程的不可或缺的一环(Hetherington & Woodward, 2003)。植物通过调节气孔导度来平衡、优化光合作用和蒸腾速率的关系。早在1927年, Scarth就针对碳的固定和水分蒸腾提出“当气孔调节一个过程的同时, 必定也在调节另外一个过程, 问题是在植物水分利用的有效策略中, 哪个过程真正体现了气孔的作用”。加强对气孔行为及调节规律的认识, 将有助于理解植被-大气间的碳水交换过程的生理学基础和水分利用策略。为此, 本文综述了植物最优气孔行为理论和气孔导度模拟的研究现状和进展, 并针对植物最优气孔行为理论和气孔导度的模拟提出了今后的研究方向和重点。

1 气孔导度模拟的研究现状

大约4亿年前, 地球上的植物就进化出了气孔组织(Edwards *et al.*, 1992)。对不同环境的适应是气孔和植物进化的源动力(Beerling, 2007)。当气孔的保卫细胞水势下降, 吸水膨胀, 气孔打开, 气孔导度增大, CO_2 和水汽就容易进出气孔; 相反, 当保卫细胞水势上升, 失水收缩, 气孔会缩小, 气孔导度减小, CO_2 和水汽就较难进出气孔; 保卫细胞持续失水, 气孔就会关闭, CO_2 和水汽就无法出入。气孔组织对多种环境和植物生理因素(如光照、温度、相对湿度、饱和水汽压亏缺、土壤湿度、大气 CO_2 浓度、呼吸速率、水势以及植物内源激素的变化)反应敏感(Davies *et al.*, 2002; Mott, 2009)。在这些因素中, 气孔对干旱的反应是科学家尤其关注的。水分胁迫对植物的生长、群落的组成以及生态系统结构和功能都有严重的影响, 尤其对农作物的产量影响巨大。在全球变化的背景下, 干旱发生的频率、程度以及可能覆盖的区域都将加大, 在特定的区域势必存在水分供应缺乏和灌溉需求增大之间的剧烈矛盾(IPCC, 2013)。理解和模拟水分缺乏条件下气孔的行为, 对设计更加有效和节水的农业灌溉系统和选择适应特定环境的农作物品种具有重要的意义。

以碳积累为代表的光合作用和以水分消耗为代表的蒸腾作用是所有植物功能模型的基础, 准确地模拟光合作用和蒸腾作用也是生态系统模型、植被模型、地球系统模型能够有效模拟碳、水和能量循环的必要条件(Wang *et al.*, 2013b, 2015, 2016)。由于以Farquhar等(1980)的光合作用模型为代表的机理模型的广泛应用, 通过对物种生物属性和环境参数(如

光合最大羧化速率(V_{cmax})、 CO_2 浓度、温度和光照)的测量, 可以有效地模拟光合作用(Wullschlegel, 1993; Kattge *et al.*, 2009)。相对于光合作用的机理模型, 蒸腾作用通常都是由经验或者半经验模型模拟出的气孔导度值来计算。过去40年里, 气孔导度的模拟工作大量开展。概括来讲, 对气孔导度的模拟有以下几种方式: (1)经验模型。大多通过气孔导度与多个环境因素如空气湿度(Lange *et al.*, 1971)、水汽压亏缺(VPD)(Monteith, 1995)、叶片温度(Jarvis, 1976; Jones, 1992)和臭氧(Uddling *et al.*, 2009)等的统计关系建立模型; (2)半经验模型。基于植物生理特性的假设, 但是仍然和经验模型结合, 如基于气孔导度和光合作用(Ball *et al.*, 1987; Leuning, 1990, 1995; Misson *et al.*, 2004b)、脱落酸(ABA) (Tardieu & Davies, 1993; Guteschick & Simonneau, 2002)、水分传导(Sperry *et al.*, 1998; Oren *et al.*, 1999; Tuzet *et al.*, 2003)和膨压调节(Dewar, 2002; Buckley *et al.*, 2003)等的关系建立的模型, 其参数不具有生物学属性; (3)机理模型。基于植物生理特性的假设, 其参数具有生物学特性, 并具有可以应用在各种环境条件下的潜力(Dewar, 2002; Medlyn *et al.*, 2011; Prentice *et al.*, 2014)。很多文献已经综述过气孔导度的经验与半经验模型, 本文将侧重阐述气孔导度机理模型的研究。

经验模型通常都忽略了叶片生理特性和气孔导度之间的关系, 也经常缺少反馈机制, 并且需要对模型参数进行大量的调试, 这些都限制了气孔导度经验模型的应用。Jarvis模型(方程1)是气孔导度经验模型, 最早由Jarvis (1976)提出, 后来经过许多学者的优化改进(Stewart, 1988; White *et al.*, 1999; Macfarlane *et al.*, 2004; Misson *et al.*, 2004a; Noe & Giersch, 2004)。

$$g_s = g_{\text{smax}} f(Q) f(T_i) f(\text{VPD}) f(\psi_{\text{pd}}) \quad (1)$$

Jarvis模型是一个多元非线性模型, 其原理是将最大的气孔导度参数值与数个环境限制因子相乘。模型中 $f(Q)$ 、 $f(T_i)$ 、 $f(\text{VPD})$ 、 $f(\psi_{\text{pd}})$ 分别代表光强胁迫、温度胁迫、水汽压亏缺胁迫和干旱胁迫。Jarvis模型形式灵活, 是第一个相对完整的气孔导度模型, 为系统地研究气孔随外界环境变化的机理创造了条件。但是此模型也具有缺陷, 包括模型中的参数大多没有生物学意义(李永秀等, 2011), 这给机理性的研究和模型解释增加了困难; 随着参数的增多, 模型的复杂程度急剧增加, 这给模型的应用增加了困难;

模型只针对于各环境因子独立作用下的气孔导度变化, 忽略了各因子之间的协同作用(牛海山等, 2005), 这一缺陷严重限制了Jarvis模型的实际应用。即便如此, Jarvis模型还是在很长一段时间里为气孔响应机理的研究指明了方向, 具有里程碑式的意义。

Ball等(1987)提出了一个半经验模型, 它基于以下实验结果: 气孔导度与光合速率和相对湿度正相关, 而与CO₂浓度负相关。该气孔模型被称为Ball-Berry模型或者BWB模型(方程2)。Leuning (1990, 1995)等在其基础上提出用水汽压亏缺(VPD)取代相对湿度可以更好地反映气孔导度对湿度的响应。

$$g_s = g_0 + m \frac{Ah}{C_a} \quad (2)$$

在方程(2)中, g_s 是气孔导度($\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), A 是光合净CO₂吸收速率($\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$), h 是大气相对湿度, C_a 是叶片表面空气CO₂浓度($\mu\text{mol} \cdot \text{mol}^{-1}$), g_0 是y轴截距, m 是直线斜率。这一由统计分析得来的基于光合作用与气孔导度线性关系的半经验模型, 因其简单、易于理解的特点被广为应用。但相对于相对湿度, 气孔导度对蒸腾作用的响应更加敏感这一现象并未在这个模型中表现出来(Eamus *et al.*, 2008)。在这个模型中, m 值并没有生物学意义, 我们只能通过大量的测量数据来探究其如何随外界因素而变化, 却不能了解其中的机理, 并且由于 m 值测定困难, 人们对不同生境、不同功能型物种的 m 值的变化规律知之甚少。

Ball-Berry模型的特点是可以把复杂的环境因子影响综合到光合作用、湿度和CO₂浓度3个要素中。它简化了气孔导度与环境因子的关系, 但是它把光合作用速率作为模型的输入参数处理, 因而无法应用这个模型直接从环境因子计算出气孔导度。Collatz等(1991)耦合了该气孔模型与光合作用生化模型, 建立联立方程组, 以便同时解出光合速率和气孔导度。Ball-Berry气孔导度模型同Farquhar等(1980)光合作用模型结合(FvCB模型), 可以有效地模拟叶片尺度光合作用和气孔导度。FvCB模型被广泛应用到大量陆地生态系统模型中, 并结合气候模式来预测全球变化对植被和大气之间碳、水循环的影响(Sellers *et al.*, 1997; Damour *et al.*, 2010)。因此这两个模型的准确性, 将直接影响大量生态系统模型、区域模型乃至地球系统模型预测的可靠性。

此后多人对Ball-Berry模型进行了优化、改进和

应用, 如加入叶片水势的作用等(Sellers *et al.*, 1992; Kim & Lieth, 2003; Tuzet *et al.*, 2003; Yu *et al.*, 2004), 但其本质上依然是半经验模型。在对Ball-Berry模型的众多改进中, Yu等(2004)的模型较为突出。此模型结合了Jarvis模型和Ball-Berry模型的优点, 采用了更便于计算的模型参数, 基于气孔与光合作用的联系及光合作用与光照之间的联系, 推导出了双曲线式的气孔导度模型, 使得直接从气象参数计算气孔导度成为可能。模型简洁、实用, 对于实测数据符合较好。

气孔导度斜率是Ball-Berry模型中一个非常重要的参数, 它很可能随植物种类、叶片养分状态等变化。Ball-Berry模型假定气孔导度斜率是一个常数, 这一点已经被后来的研究否定, 对于单个物种而言, 气孔导度斜率在一段生长期保持内保持稳定, 但对于不同物种, 气孔导度斜率会有所差异, 并且该斜率值与气孔导度的数值有显著相关关系(Yu *et al.*, 2004)。在过去大约30年间, 生态系统模型通常都假定一个常数来代表所有C₃植物的 m 值或者通过手动调整来拟合观测数据($m = 6$, Wang *et al.*, 2013b)。考虑到影响气孔导度的其他叶片性状在不同物种间存在着很大的变异性, 假定C₃植物的 m 值是一个常数是不切实际的。气孔导度模拟的微小误差, 上升到生态系统或者全球尺度, 都有可能造成极大的谬误。通过对模型参数敏感性分析和由参数导致的模型不确定性的方差分解分析可知: 在14个被考虑的模型参数中, 气孔导度斜率对于模型不确定性(杨树(*Populus* spp.)净初级地上生产力(ANPP))的贡献位列第二, 仅次于生长呼吸(Dietze *et al.*, 2014)。虽然Dietze等(2014)的研究只分析了一个陆地生态系统模型(Ecosystem Demography 2)的模拟结果, 但由于很多模型都利用相似的光合作用和气孔导度模型, 因此可以推测相似的结果可能也会发生在其他生态系统模型的模拟中, 而当采用这些模型预测蒸腾作用和水通量时, 气孔导度斜率对模型不确定性的贡献将会更大。

目前盛行的生态系统模型多是通过减小 m 值来模拟干旱对气孔导度和光合作用的影响(Wang *et al.*, 2013b, 2015); 或者通过减小光合作用模型中的 V_{cmax} 来间接地减小气孔导度和光合作用来实现干旱条件下的生长模拟(Krinner *et al.*, 2005)。没有叶片尺度上气孔导度模拟的准确性, 陆地生态系统模型将无法准确地预测冠层、生态系统乃至区域尺度上碳、水

循环的变化(Damour *et al.*, 2010)。成功模拟气孔行为的机理模型将为理解碳水耦合的适应过程以及陆地植被模型对植被结构、功能和演替的准确把握提供一个有效的框架。

2 最优气孔行为理论和气孔导度机理模型

最优气孔行为理论认为气孔的最优化行为就是在某一时间段内, 最大化光合碳固定的同时最小化蒸腾作用, 也就是说, 对于一定的水分消耗, 最大化光合碳固定, 或者也可以说, 对于一定的碳固定(A)而言, 最小化蒸腾作用(E), 即最大化 $A - \lambda \times E$ 或者最小化 $E - 1/\lambda \times A$ (Cowan & Farquhar, 1977)。其中 λ 是临界水分利用效率(marginal water use efficiency), 也就是植物损耗单位水的碳生产量($\partial A/\partial E$, mol CO₂·mol⁻¹ H₂O), 实验证明这一数值在一定时间内不会随温湿度变化而改变(Hall & Schulze, 1980; Field *et al.*, 1982), 但是会因土壤含水量减小而下降(Farquhar *et al.*, 1980)。最优气孔理论被广为接受, 而且可以为气孔导度模型所借鉴, 以研究不同环境和生物因素对气孔行为的影响。然而由于对 λ 的有限理解及由其所推出的模型无法准确描述气孔对CO₂的响应规律(Thomas *et al.*, 1999), 这一理论还没有得到广泛应用。

依据最优气孔导度理论并借鉴Ball-Berry的半经验模型发展的气孔导度机理模型(推导过程见Medlyn *et al.*, 2011)(方程3), 可以将模型中的斜率参数与广受肯定的最优气孔理论中的临界水分利用效率($\lambda = \partial A/\partial E$, mol CO₂·mol⁻¹ H₂O)(Damour *et al.*, 2010; Medlyn *et al.*, 2011)联系在一起(方程4), 使得模型参数具有重要的生物学含义。

$$g_s = g_0 + 1.6 \left(1 + \frac{g_1}{\sqrt{D}} \right) \frac{A}{C_a} \quad (3)$$

方程(3)中 D 是饱和水汽压亏缺值(kPa), g_1 是与方程(1)中 m 值相关的模型参数, 在本文中我们称之为气孔导度斜率(stomatal slope)。

Medlyn 等(2011)的机理模型与Ball-Berry和Leuning的半经验模型相比, 其对气孔导度的模拟更加准确, 且模型中的 g_1 与临界水分利用效率具有一定的比例关系(方程(4)), 这一参数因此具有了生物学含义, 可以用来描述植物的水分利用策略(Medlyn *et al.*, 2011; Hérault *et al.*, 2013)。

$$g_1 \propto \sqrt{\Gamma/\lambda} \quad (4)$$

式中 λ 是临界水分利用效率, Γ 是不计算暗呼吸的CO₂补偿点浓度(μmol·mol⁻¹)。方程(3)显示气孔导度斜率将随着临界水分利用效率的升高而降低, 随CO₂补偿点的升高而升高。

3 气孔导度斜率和临界水分利用效率的影响因素

3.1 植物功能型和物种

不同植物功能型的气孔导度斜率值大多差异较大, 农作物的气孔导度斜率值最大, 裸子植物树种的斜率值最小(Zhou *et al.*, 2013)。Medley等(2011)比较了8种不同物种的气孔导度斜率, 发现被子植物气孔导度斜率高于针叶树种。Lin等(2015)发现: 对于被子植物来说, 随着植物干材密度的增加, 气孔导度斜率值会下降, 而裸子植物却没有这样的规律。这可能与被子植物提供支撑作用和水分运输作用的是两套系统, 而裸子植物中管胞同时提供了这两项功能相关(Hacke *et al.*, 2001)。Way等(2014)发现: C₃植物与C₃-C₄中间体植物相比, 临界水分利用效率并没有显著差异, 而具有C₄循环的近C₄中间体植物的临界水分利用效率比C₃-C₄中间体植物显著增强。

实验数据也显示不同种植物在同样湿润的环境下气孔导度斜率不同, 对外界水分条件变化的响应也不同(Zhou *et al.*, 2013)。气孔导度斜率值较低的植物在同样的外界环境下能达到更低的气孔导度, 小幅度降低气孔导度会显著升高水分利用效率, 这样一种利用少量水生产生物量的能力(水分利用率)有利于它们在干旱无灌溉或水分供应不足的地区生存(Hetherington & Woodward, 2003; Somerville *et al.*, 2010)。而高气孔导度的植物光合收益低, 且当气孔导度发生较大改变时, 叶温改变较小, 水分消耗大, 只适宜生存在水分供应充足的地区。同一植物功能型中的不同种植物, 也会有很多属性上的不同。Wang等(2013b)在同质园中种植并测量了17种不同树种的生长和生理参数, 发现不同物种的气孔导度斜率存在较大差距(图1)。这也是许多生态系统模型使用固定的气孔导度斜率值而使预测存在偏差的一个重要原因(Smith & Dukes, 2013)。

3.2 生境条件

对于外界环境的变化, 气孔导度斜率也会做出

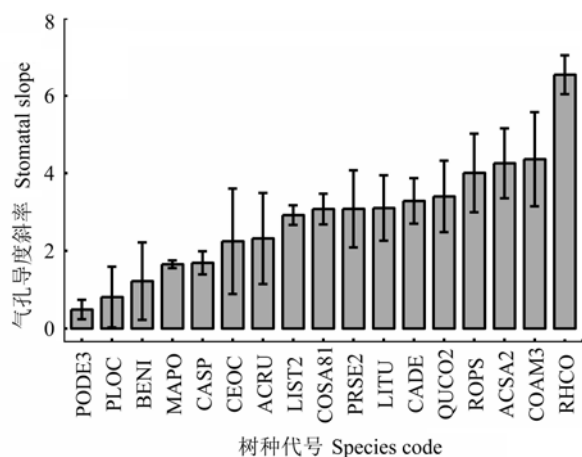


图1 用Medlyn气孔导度机理模型(Medlyn *et al.*, 2011)计算的17种树种的气孔导度斜率(平均值 \pm 标准误差, $n = 3$)。ACRU, 红花槭; ACSA2, 糖槭; BENI, *Betula nigra*; CADE, *Castanea dentata*; CASP, 黄金树; CEOC, 美洲朴; COAM3, *Corylus americana*; COSA81, *Cornus sanguinea*; LIST2, 北美枫香美国香枫; LITU, 北美鹅掌楸; MAPO, 桑橙; PLOC, 一球悬铃木; PODE3, *Populus deltoides*; PRSE2, 野黑樱桃; QUCO2, 猩红栎; RHCO, *Rhus copallinum*; ROPS, 刺槐。

Fig. 1 Variation of stomatal slope among 17 tree species calculated by Medlyn *et al.* (2011) (mean \pm SE, $n = 3$). ACRU, *Acer rubrum*; ACSA2, *Acer saccharinum*; BENI, *Betula nigra*; CADE, *Castanea dentata*; CASP, *Catalpa speciosa*; CEOC, *Celtis occidentalis*; COAM3, *Corylus americana*; COSA81, *Cornus sanguinea*; LIST2, *Liquidambar styraciflua*; LITU, *Liriodendron tulipifera*; MAPO, *Maclura pomifera*; PLOC, *Platanus occidentalis*; PODE3, *Populus deltoides*; PRSE2, *Prunus serotina*; QUCO2, *Quercus coccinea*; RHCO, *Rhus copallinum*; ROPS, *Robinia pseudoacacia*.

不同的响应。不同植物物种的水分利用策略不同, 在同样的湿度环境下气孔导度斜率会有差异, 同样的物种在不同水分环境下气孔导度斜率也会不同(Zhou *et al.*, 2013)。Lin等(2015)对超过1万条光合测量数据综合分析后发现, 在植物生长适宜的外界温湿度下, 随着温湿度升高, 气孔导度斜率都会增加。对于气孔导度斜率随温度升高而增加的原因, 有两种解释: 一是气孔导度斜率与 CO_2 补偿点浓度相关(Medlyn *et al.*, 2011), 而这一浓度会随温度升高而增加(Bernacchi *et al.*, 2001); 二是水分子黏性会随温度升高而降低, 这就降低了运输水分的消耗, 从而增高了气孔导度斜率(Prentice *et al.*, 2014)。Hérault等(2013)报道了产地不同的4种桉属植物在相同环境条件下, 气孔导度斜率随着自然产地不同而不同, 自然生长在湿润地区的植物气孔导度斜率比在半湿润地区的植物高。在湿润环境生长的长叶松(*Pinus palustris*)气孔关闭对增加的饱和水汽压亏缺的反应

比在干旱环境下更加敏感(Addington *et al.*, 2006)。

3.3 CO_2 浓度升高

虽然光合作用、气孔导度的调查数据在文献中大量存在, 但是由于实验设计不同以及缺少饱和水汽压亏缺等环境参数的信息, 很少有实验数据能够满足对气孔导度斜率进行模拟计算的要求(Zhou *et al.*, 2013)。以往大多数关于气孔导度斜率的研究都是在温室里的短期试验, 在自然条件下的研究还很少(Medlyn *et al.*, 2011)。对于增高的 CO_2 浓度下气孔导度对环境因子的适应性变化的研究结果也不一致。在高 CO_2 浓度的未来环境下, 植物会降低气孔导度和提高光合速率(Long *et al.*, 2004; Bernacchi *et al.*, 2005)。有学者在培养箱中升高 CO_2 浓度对大豆(*Glycine max*)和棉花(*Gossypium hirsutum*)进行培养研究得出, 气孔导度斜率会因 CO_2 浓度的增加而降低(Harley *et al.*, 1992; Bunce, 2004)。但是Leakey等(2006)在FACE (free-air CO_2 enrichment)实验样地对大豆进行了生长和生理参数测量, 他们的实验结果却表明气孔导度斜率不会因外界 CO_2 浓度的升高而改变, 并且指出前人所得的气孔导度斜率降低的结论可能是增高的 CO_2 浓度对气孔导度带来的瞬时改变的结果。Medlyn等(2001)也测定了生长在高 CO_2 浓度下6种不同树种的生理参数, 发现 CO_2 浓度升高并没有改变气孔导度斜率。这一结果也在Katul等(2009)的研究中得到证实, Katul等(2009)也发现 CO_2 浓度升高并没有改变Ball-Berry模型中的光合作用与气孔导度的线性关系的斜率。

3.4 土壤干旱

在很多生态系统模型中, 土壤干旱胁迫对气孔导度影响的模拟通常是通过改变水分胁迫与光合作用/气孔导度之间的作用关系来实现的(Sala & Tenhunen, 1996; Verhoef & Allen, 2000)。但也有模型是通过改变水分胁迫与光合作用或者光合作用参数 V_{cmax} 和最大电子传输速率(J_{max})的关系, 模拟水分胁迫下光合作用的改变进而模拟气孔导度的改变(Sellers *et al.*, 1996; Ronda *et al.*, 2001; Best *et al.*, 2011)。虽然在轻度干旱情况下, 上述几种做法可以模拟出水分胁迫对叶片尺度碳水通量的影响, 但在严重干旱情况下无法同时准确模拟光合作用和蒸腾作用(Verhoef & Allen, 2000; Reichstein *et al.*, 2002; Keenan *et al.*, 2009)。Egea等(2011)提议, 在干旱条件下可以通过先限制叶肉导度, 进而限制气孔导度和光合作用参数

的方案来提高光合作用和气孔导度模拟的准确性。Zhou等(2013)的研究结果也表明模拟干旱状况下的气孔导度, 必须同时考虑干旱对气孔和非气孔因素(如 V_{cmax})的综合影响。由于对于干旱状况下气孔导度预测的不准确性, 现有的模型一般都倾向于高估光合作用和蒸腾作用对干旱的响应(Dietze, 2014)。与以前从气孔(物理过程)或者非气孔(生化过程)的角度出发研究干旱对光合作用和气孔导度的影响不同, 气孔导度机理模型中的气孔导度斜率在干旱环境下的变化规律包含了干旱对气孔(生物物理因素)和非气孔因素, 包括最大光合效率和临界水分利用效率的综合影响, 为研究全球变化下陆地生态系统碳-水耦合的适应性提供了一个简明且综合的框架。Manzoni等(2011)计算了50种植物的临界水分利用效率, 发现在忽略表皮水分丢失的情况下, 植物临界水分利用效率在轻微干旱的情况下增高, 而在严重干旱的情况下下降; 如果不忽略表皮水分丢失, 植物临界水分利用效率会随着水分胁迫的增加而提高; 而不同的植物功能型和不同的气候条件下, 反应也会不同。总体说来, 土壤水分较少时, 植物的水分利用效率会增高, 此时气孔导度斜率值也会降低(Lin *et al.*, 2015)。在环境水分条件与气孔导度斜率的变化规律之间还有很多值得讨论的地方, 我国学者对于水分利用的研究主要集中在单叶水分利用效率(付士磊等, 2006; 杨建伟等, 2006; 全先奎和王传宽, 2015)、气孔导度时空变异的调查(司建华等, 2008)、气孔导度对水分环境的响应(鱼腾飞等, 2012; 袁国富等, 2012)、单叶或者幼苗蒸腾速率(宋炳煜等, 2004; 岳广阳等, 2009)、树干液流密度(赵平等, 2006)、土壤水分定位监测(尹春梅等, 2008), 以及涡度协相关法测量生态系统水分利用效率(Zhou *et al.*, 2013)等方面。土壤干旱如何影响不同功能型和物种的气孔导度斜率和临界水分利用效率, 还有待于进一步的研究。

3.5 生物因素

以往研究显示叶片水势(Oren *et al.*, 1999)、叶片、枝条、根部和整株植物水力传导(Salleo *et al.*, 2000; Addington *et al.*, 2004; Bunce, 2006; Domec *et al.*, 2009)、叶片相对含水量(Ewers *et al.*, 2005)等会影响气孔导度对饱和水汽压亏缺的响应。而由于树龄和树高都会影响水力传导和气孔导度, 进而都会影响气孔导度斜率(Schäfer *et al.*, 2000; Franks, 2004; Ewers *et al.*, 2005; Buckley & Roberts, 2006; Ambrose

et al., 2010; Woodruff *et al.*, 2010)。木材密度和气孔导度斜率之间也存在着显著的负相关关系(Hérault *et al.*, 2013; Lin *et al.*, 2015)。植物结构属性, 如根叶比、根深等以及水力传导结构属性也会影响气孔导度斜率(Litvak *et al.*, 2012; McCulloh & Woodruff, 2012)。如与散孔材木相比, 环孔材木的气孔对环境因素变化的反应更加敏感(Bush *et al.*, 2008), 但是在Litvak等(2012)的研究中并未发现木材结构影响气孔导度斜率的现象。而随着测量高度的增高, 气孔导度对饱和水汽压亏缺响应的敏感性也会降低。叶肉导度和 V_{cmax} 也通过影响光合作用影响植物的水分利用效率(Wang *et al.*, 2013a)。Flexas等(2013)分析了44种不同物种水分利用效率的规律, 发现水分利用效率和叶肉导度与气孔导度的比值成正比。这个关系表明水分利用效率只有在固碳能力的提高高于水分丢失增加(气孔导度升高)的情况下, 才可以升高。可以预测, 同样的关系也应该在气孔导度斜率及 V_{cmax} 和气孔导度的比值间存在。临界氮利用效率也被证明和临界水分利用效率有互补的关系(Palmroth *et al.*, 2013)。

气孔导度斜率的大小与气孔导度和气孔密度有关(Oren *et al.*, 1999; Pataki & Oren, 2003; Ewers *et al.*, 2008)。当气孔导度较小时, 一点小小的改变就会给叶温带来极大的影响, 这时的气孔表现极其敏感。最高气孔导度斜率往往出现在0.4以下的低气孔导度条件下, 0.4以上的气孔导度, 响应机制会变得比较平缓(Hetherington & Woodward, 2003)。

实验观测也表明气孔导度斜率与黎明叶片水势之间存在指数关系, 通过实验数据拟合可以得出二者之间的经验方程(Mäkelä *et al.*, 1996; Tuzet *et al.*, 2003; Zhou *et al.*, 2013)。

$$g_1 = a \times \exp(b\psi_{\text{pd}}) \quad (5)$$

式中 ψ_{pd} 是黎明叶片水势(MPa); a 和 b 均是拟合参数: a 是 $\psi_{\text{pd}} = 0$ 时的 g_1 值, b 代表了 g_1 对 ψ_{pd} 的敏感程度。

除了以上因素以外, 还有没有其他的生物和非生物因子, 如氮磷添加、 O_3 浓度和气溶胶浓度升高等会造成气孔导度斜率的改变, 目前还缺少相关的研究成果。

4 气孔导度机理模型的应用

大多数地球系统模型或者植被模型都采用经验或者半经验模型来模拟气孔导度(Sellers *et al.*, 1992, 1997; Bonan, 1995; Wang *et al.*, 2013b, 2015)。虽然对

于经验或半经验模型来说, 可以利用实验数据矫正参数, 但是在现实中, 并非如此。如上文中所提到的, 多数模型都只是区分了C₃和C₄植物的气孔导度模型参数 m 值(Krinner *et al.*, 2005; Oleson *et al.*, 2013)。De Kauw等(2015)首次将气孔导度机理模型(Medlyn *et al.*, 2011)耦合到陆地表面模型CABLE (Community Atmosphere Biosphere Land Exchange)中, 研究结果显示: 相比于气孔导度经验模型, 耦合气孔导度机理模型导致在常绿针叶林、苔原和C₄草原区域, 年蒸腾量减少了30%。Kala等(2014)进一步耦合气孔导度机理模型、CABLE和ACCESS (Australian Community Climate and Earth Systems Simulator)模型, 研究结果显示在北半球的夏季, 新的模型预测的温带森林潜热通量每天减少0.5–1.0 mm, 直接导致每天最高和最低温度升高了1 °C, 而极端高温升高了1.5 °C。地表的能量平衡也将进一步影响净初级生产力和陆地碳平衡。由此可见, 深入研究气孔导度斜率的变化规律并提高气孔导度预测的准确性, 可大大减小生态系统模型对碳水通量预测的不确定性, 这对区域尺度生态系统碳水平衡的研究至关重要。然而, 由于对气孔导度斜率变化规律的理解还十分有限, 气孔导度机理模型在植被和地球系统模型中的应用还需要加强。

5 最优气孔导度行为理论和气孔导度机理模型研究的未来展望

气孔行为决定了植被碳、水循环的耦合过程, 因此准确模拟气孔行为是预测全球变化对植被结构和功能影响的关键。从由气孔导度和环境及植物生理因素的统计关系发展的经验模型到可以囊括多个环境因素、拥有理论基础并且具有生物学意义参数的机理模型, 气孔导度的模拟已经取得了一定的进展。叶片尺度气孔行为和水分利用特征及其影响因素的深入研究, 对于理解特定区域, 特别是干旱半干旱地区植被对环境的适应机制以及预测气候变化条件下气孔导度调节水分利用的动态和指导农林管理具有重要的理论和实践意义。为更好地推进气孔导度行为的研究, 在各种环境条件下准确模拟气孔导度, 需要在以下几个方面加强研究:

(1)探索不同气候区带, 不同功能型、物种、品种等气孔导度斜率以及临界水分利用效率随环境变化的规律;

(2)探索气孔行为与叶片经济效率、水力传导、固碳效率和氮利用效率等指标之间的普适性权衡关系, 以深入理解抗旱植物决定气孔行为的内在因素;

(3)探索和量化全球变化背景下, 特别是在土壤水分条件变化情况下气孔行为的变化规律, 对于理解植被生态系统对全球变化的响应和适应机制, 以及预测未来全球变化背景下植物和大气间的碳水交换都有重要意义;

(4)加强气孔导度机理模型和植被模型、陆地表面模型, 以及地球系统模型耦合, 提高模型预测碳水通量的准确性。

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